On Deterministic and Stochastic Models of Kleptoparasitism

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Abstract:

Kleptoparasitism, the stealing of food items, is a common biological phenomenon that has been studied mostly with the help of deterministic dynamics for infinite populations. The infinite population assumption takes the models far from the biological reality. In this paper we provide a review of the main theoretical works on kleptoparasitism and then focus on the stochastic dynamics of kleptoparasitic individuals in finite populations. We solve the dynamics analytically for populations of 2 and 3 individuals. With the help of numerical solution of the dynamics, we were able to conclude that the behavior of the uptake rate in the population is mostly determined by the uptake rates at populations of 2 and 3 individuals. If the individuals do better in a pair, then the uptake rate is a decreasing function of the population size. If the individuals do better in a triplet than in a pair, then the uptake rate is a zigzag function with lows for even population sizes and ups for uneven population sizes.

Keywords: Kleptoparasitism | game theory | strategy | finite populations

Article:

1. Introduction

Kleptoparasitism is a behavior in which one organism steals food or other resources that another organism has caught, killed, or otherwise prepared for its own use. This process occurs across a great diversity of taxa, with recent observations from large carnivorous mammals [11], seabirds [13], scavenging bird guilds [3], insects [23], fish [14], lizards [12], snails [17] and spiders [27, 28, 1, 18].

When considering kleptoparasitism we must ask, why would a species evolve this behavior? From an evolutionary standpoint the answer to this is quite logical: in order for a behavior to evolve in a population through natural selection, the individuals who follow this behavior must

enjoy greater reproductive success (higher fitness) compared to others in the population, and this trait must be passed on to their future offspring. Since not all species that seem capable of kleptoparasitism show it, and since there is strong variation between and within species in the extent to which this tactic is used, there is a need for a predictive theoretical basis to explain this variation. Hence there has been a considerable body of theory aimed a predicting the evolutionarily stable use of kleptoparasitism in different ecological circumstances.

In this paper we first review seminal theoretical papers focused on intraspecific kleptoparasitism, and then study the stochastic model introduced in [29] with a special focus on small population sizes. Almost all models developed to date are deterministic, based on a certain system of *ordinary differential equations* (ODEs). Consequently, these models assume a very large population size. On the other hand, the majority of model organisms that exhibit kleptoparasitism are birds, mammals and fish, with relatively small populations that are likely to violate assumptions of infinite population size models. To our knowledge, only two papers to date [22] and [29] proposed stochastic models for finite and thus potentially small populations. Moreover, [22] deal with a model that differs from the mainstream deterministic models and [29] focuses on situation for medium population sizes. Hence, models that can accurately describe kleptoparasitism in smaller population sizes are needed.

2. Deterministic models of kleptoparasitism

In this section, we provide an overview of the main models and summarize the major assumptions and conclusions of each.

2.1 *Holmgren, 1995*

One of the first models focused on intraspecific kleptoparasitism was developed in [16] and it used foraging interference as its basis. In this model, an individual's behavior was deterministic, always fighting whenever an individual encountered another individual who had a food item. The model also had individuals encountered each other randomly but at a constant rate. Because individuals were distinct, it allowed for one to examine the effect of a given type of individuals who differed in their dominance over each other. But the model was very complex and only allowed for a numerical, but not analytical, solution.

2.2 *Stillman et al., 1997*

In [26], the authors extended the existing behavior-based foraging interference models to kleptoparasitism. In their model, an individual could engage in one of four behaviors: searching, handling, fighting or avoiding. Their model had three key components:

- the response of an individual to a competitor was not fixed,
- individuals did not move randomly, and
- that time was not the only currency by introducing prey as another form of currency.

The authors applied the model to data collected on foraging shorebirds including oystercatchers, curlew, and knots. They found the model to be robust, accurately predicting interference 85% of

the time. The authors suggested that future models should incorporate the idea that an individual follows optimal decision rules when deciding their behavior. Two major limitations of this paper include the assumptions that prey items were identical, and that the handler always defended the prey.

2.3 *Ruxton and Moody, 1997*

In [25], authors took the advice given in [26] and used a functional response model to bridge the gap between an individual's behavior and the evolution of a population. Their approach allowed for an analytical solution of the model, not just a numerical one. In this model, individuals in the population were engaged in one of the following behaviors:

- searching for a food item,
- handling a food item, ² winning a contest over a food item,
- losing a contest over a food item. The fight over a food item resulted when a searcher found a handler.

The model examines an individual's behavior over varying densities of prey and competitors and when there is more than one patch of food. It predicts that the proportion of individuals wanting to forage in the best patch will always be greater than the proportion of prey available. It also predicts that an individual's decision to forage in a given patch is dependent on two things: the proportion of food in that patch and the distribution of food between other patches in the area. Two major limitations of this model were that: (1) individuals have equal competitive ability, and (2) any time a forager encountered an individual handling a prey item, it would attempt kleptoparasitism.

2.4 *Broom and Ruxton, 1998*

In [9], authors take a different tack than [25]. They divide the individuals in the population into three mutually exclusive groups:

- searching for a food item or for a handler,
- handling a food item,
- fighting over the food item.

They assumed that individuals can adopt different strategies (to steal or not to steal) and they examined what strategies can be evolutionarily stable. An *evolutionary stable strategy* (ESS) is a strategy which if adopted by a population cannot be invaded by any competing alternative strategy, [20].

The situation can be described by the diagram on Figure 1. It should be noted that the model assumes that a food is a shell type (see Section 2.6), i.e., handled for an exponentially distributed time; and that the fights last for an exponentially distributed time.

There are two main advantages to assuming the exponentially distributed time for handling.

(1) One can use ODEs in the model,
(2) The food item has always the same value until eaten.

The latter is a consequence of the fact that the conditional expectation for an exponentially distributed random variable is the same as the original expectations. Once a handling starts, the expected time to finish handling is defined as Th . Provided the individual did not finish handling in the time $t0$, then at time $t0$, the expected time to finish handling is again Th . This means, in particular, that the individuals can fight over the food item as long and as many times as they choose, yet the winner always get the same food item as it would get by finding it by itself.

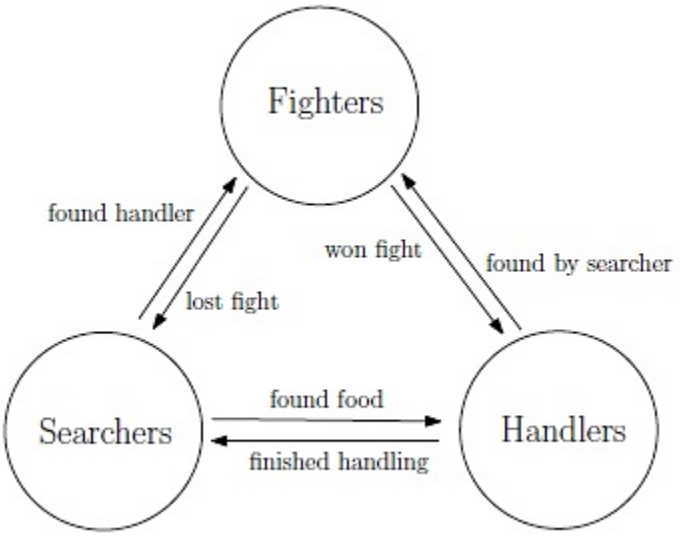

Figure 1. Schematics of the deterministic dynamics model

Using a functional response framework, the model predicts an individual's behavior under varying prey densities. If food is plentiful, the model predicts that no kleptoparasitism will take place. Once the food density drops below a critical threshold, kleptoparasitism will occur whenever the opportunity arises.

The model assumes that the behavior of an individual is deterministic; individuals either always steal or never steal, and which strategy they employ depends on either food availability or the time (length) of the encounter. The model predicts that individuals will cross a threshold level where stealing is optimal when fights are not costly and when food is hard to find. One peripheral assumption of the model, that a food item requires a specific handling time prior to receiving the energy reward, is further explored in subsequent models.

The paper [9] is a foundation for a vast majority of subsequent papers.

2.5 *Ruxton and Broom, 1999*

The model in [24] examined the trade off between investing time (or energy) in finding food on their own or by kleptoparasitizing from others. Specifically, they examined the assumption that the time of a contest over a food item is fixed. Their model suggests that the ESS will be the result of a combination of the length of time an individual is willing to compete for a food item, paired with the probability of engaging in a contest over a food item. As in [9], they assume individuals in a population can be doing one of three mutually exclusive behaviors: searching, handling, or fighting. The model shows that individuals should engage in a fight over a food for the same amount of time as, on average, it takes that individual to find a food by itself. It also predicts that, in a situation where there is a trade-off between food finding ability and the opportunity to engage in kleptoparasitism, an individual should never kleptoparasitize.
In essence, in this situation, kleptoparasitism is not an ESS. The paper, though, introduces the opportunity to test some of the explicit predictions.

2.6 *Broom and Ruxton, 2003*

In [10], the authors introduce a variant to [9] and [24] by introducing three food types:

- shells
- oranges
- apples

The shell type is a classical food model used in all previous papers and discussed in detail in Section 2.4. In short, a shell has to be broken in order to eat the food. If the shell is not broken, the expected time to break it is always the same, no matter how long one tried to open it beforehand.

The orange type of food needs to be peeled and then it can be eaten instantly. The major difference between the shell and an orange is that the orange increases in value the more it is peeled (whereas the value of an unopened shell is constant). Hence, it pays off more to try to kleptoparasitize an almost peeled orange than an unpeeled orange. Consequently, one should kleptoparasitize when the original handler is almost done. In this case, kleptoparasitism should decrease as foraging density increases.

The apple type of food can be eaten the moment it is found. The longer one eats the apple, the lower will be the value, and it is assumed that the value continuously decreases to 0. Consequently, it is better to attack early in the handling time and kleptoparasitism should increase as foraging density increases.

2.7 *Luther and Broom, 2004*

In all of the previous papers, it was assumed that the population can achieve an equilibrium, i.e., almost constant densities of individuals in various states. In [19] the authors examined this assumption and they found that:

(1) at low densities, the population reaches equilibrium quickly,

(2) at high densities the rate at which the population reaches equilibrium is influenced by the value of the handling time, and
(3) when the behavioral state of kleptoparasitism is added it severely complicates model (by adding a nonlinearity to the system of ODEs) but that equilibrium is eventually reached.

The addition of other behavioral states (such as resting/recovering) only increases the time of convergence to the equilibrium by a factor that is dependent on the number of behavioral states. Another important conclusion [19] drawn is that the speed of convergence depends upon two key variables: the size of the transition rate and the pattern for transition between behavioral states. In any case, the convergence was shown to be exponentially fast and thus this paper justifies the studying the kleptoparasitic population in equilibrium.

2.8 *Broom, Luther and Ruxton, 2004*

In [6], the generality of the original model of [9] was expanded in two ways:

- allowing flexibility in the likelihood that an attacker will be able to successfully steal a prey item from a handler (originally, the likelihood was 0.5),
- allowing attacked individuals the flexibility to surrender items without a time-consuming contest.

Depending on the biological parameters of the model, three different types of ESSs were possible: one where individuals both attacked others for food items and resisted attacks from others (Hawk), one where individuals attacked but did not resist (Marauder), and one where individuals did not attack, but would resist if themselves attacked (Retaliator). Further, in some circumstances, more than one of these alternate ESSs was possible, depending on the history of the system as well as its current parameter values. The Marauder ESS is particularly interesting ecologically, giving an economic explanation for one individual to surrender a valuable food item without a fight to another individual in the absence of dominance hierarchies or intrinsic asymmetries in competitive abilities between individuals.

2.9 *Recent development*

In [7] the authors used the underlying adaptive dynamics model, [21] to show how and under what conditions the different strategies of Hawk, Marauder, Retaliator and Dove studied in [6] could evolve.

In all previous papers it was assumed that the population consists of the same type of individual, i.e., every individual adopts the same strategy as anybody else. This assumption was relaxed in [5] where authors introduce a model where individuals can adopt any stealing/defending strategy.

Also, until now it has been assumed that the fights over the food items are happening only between a pair of individuals. This assumption is not valid for a variety of animals (e.g., seagulls) and a model that allows fights between many individuals was developed and studied in [8].

3. Stochastic models of kleptoparasitism

Unlike the case of infinite populations, there are only two papers on kleptoparasitism in finite populations, [22] and [29].

In [22], the authors investigate a population in which contests occur not only over the food items but also between any two individuals who are engaged in searching. This can be justified by territorial behavior of certain animals; in [22] they focused on shorecrabs *Carcinus maenas*, feeding on mussels *Mytilus edulis*. Their model predicts a zigzag type of functional response, with relatively low intake rates when the number of predators is even and high intake rates with an uneven number of predators.

In [29], the authors take the classical model [25, 9] and modify it for finite populations. They were able to find numerical solutions to their model as well as derive a normal approximation method that can be used when the population size is not too small.

In the subsequent sections we introduce and study this stochastic model in detail and derive new results.

4. Stochastic dynamics in finite populations

We consider a population of n individuals. We follow the standard model as introduced in [9] and adapted to finite population in [29]. Each of the n individuals can be in one of the following states

- searching for a food item or a handler,
- handling the food item,
- fighting over the food item with another individual.

Once a food item is found (which is happening with an average speed $v_f f$), the individual starts to handle it, i.e. preparing to eat it. The handling time is exponentially distributed, with mean Th. Once the item is properly handled, the item is eaten instantly and the individual returns to searching. If a searcher encounters a handler (which is happening at rate $v_h H$, where H is the number of handlers), these two individuals engage in a fight over the food item. The fight time is exponentially distributed with mean Tc . At the end of the fight, one individual emerges as a winner and starts handling the item, the other individuals will be searching. The summary of model parameters and notation is given in Table 1.

Table 1. A summary of model parameters (top section) and notation (bottom section)

Notation	**Meaning**
n	number of individuals in the population
$v_f f$	rate that food items are found
$1=Th$	rate that food items are handled
$1=Tc$	rate that fights are resolved

v*h*	rate that handlers are found
S	number of searchers
H	number of handlers
Pa,b(*t*)	probability there are *a* searchers and *b* handlers at time *t*
Pa,b	probability there are *a* searchers and *b* handlers in equilibrium
SaHbFn¡(*a*+*b*)	state with *a* searchers and *b* handlers
f (*n*)	proportion of handlers in the population

It is assumed that the searchers are looking for both food and handlers at the same time. If the food is found first, the searcher becomes a handler. If the handler is found first, the searcher engages with the handler in a fight over the food item.

We are interested in the proportion of handlers in the population, since this has been shown to be proportional to the uptake rate, [9].

We model the dynamics as a continuous time Markov chain. The state of the population can be described by a pair (*a*, *b*) where *a* is the number of searchers and *b* is the number of handlers. Since there are *n* individuals in total, the number of individuals engaged in the fight is given by *n* - (*a*+*b*) . Sometimes we refer to the state (*a*, *b*) by *SaHbFn* - (*a*+*b*). Only states satisfying

$0 \leq a, b, (a + b) \leq n$ and $n - (a + b)$ is even (1)

are admissible states of the dynamics, no other states can ever be attained. The scheme of the dynamics with all the transition rates is given at figure 2.

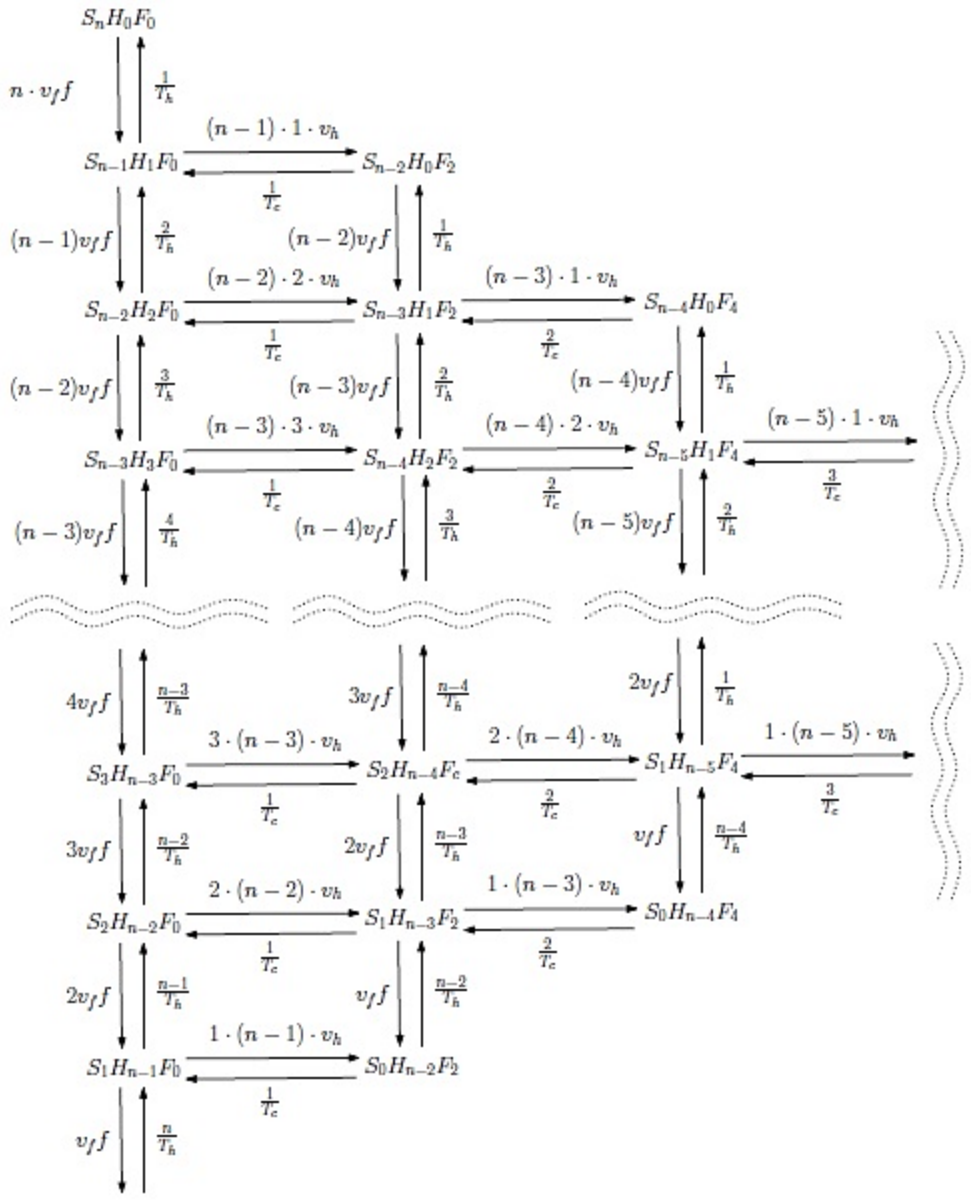

Figure 2. Scheme of the dynamics

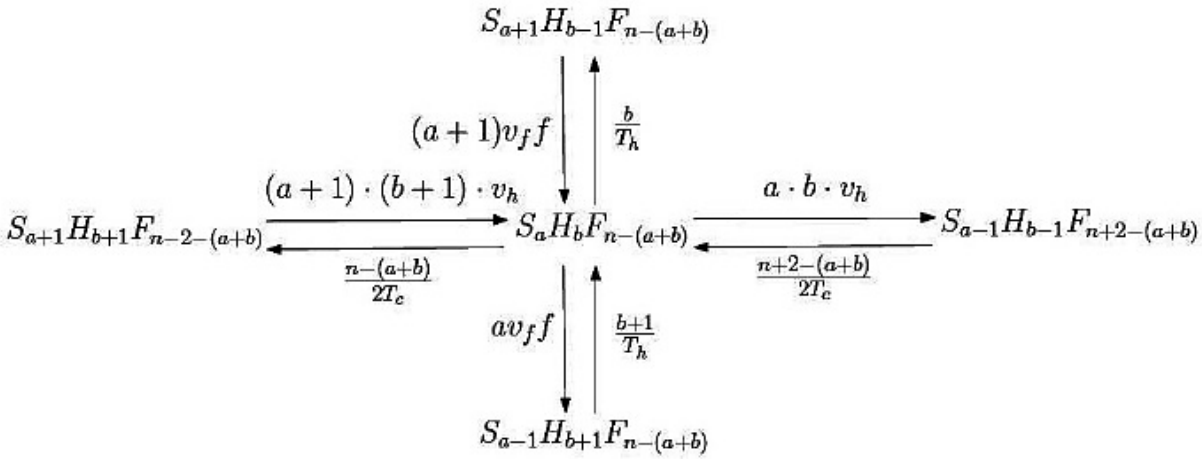

Figure 3. Detail of the dynamics

We denote the probability that the dynamics is in state (*a*, *b*) at the time *t* by *Pa*,*b*(*t*) ; in an equilibrium, we denote it just by *Pa*,*b* . The probability distributions follow the following set of Kolmogorov equations:

$$\frac{\mathrm{d}}{\mathrm{d}t}P_{a,b}(t)=\sum_{i,j=\pm 1}\left(-P_{a,b}(t)V_{(a,b)\to(a+i,b+j)}+P_{a+i,b+j}(t)V_{(a+i,b+j)\to(a,b)}\right), \quad (2)$$

where *V*(*a*,*b*)*!*(*c*,*d*) denotes a transition rate between from a state (*a*, *b*) to a state (*c*, *d*) . It is assumed that transitions rates to and from nonadmissible states are 0. If all states (*a*, *b*) and (*a*§1, *b*§1) are admissible, the dynamics is described by the scheme on Figure 3 and

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}P_{a,b}(t) \;=\; & -P_{a,b}(t)\left(\frac{b}{T_h}+ab\nu_h+a\nu_f f+\frac{n-(a+b)}{2T_c}\right)\\ & +P_{a+1,b-1}(t)\cdot(a+1)\nu_f f+P_{a-1,b-1}(t)\frac{n+2-(a+b)}{2T_c}\\ & +P_{a-1,b+1}(t)\frac{b+1}{T_h}+P_{a+1,b+1}(t)\cdot(a+1)(b+1)\nu_h\,.\end{aligned}$$

We assume “the boundary conditions” given by

Pa,*b*(*t*) = 0, if (*a*, *b*) not admissible, i.e. does not satisfy (1)
V(*a*,*b*)→(*c*,*d*) = 0, if (*a*, *b*) or (*c*, *d*) not admissible (3)

The system (2) is a system of linear ordinary differential equations. In an equilibrium, the time derivatives are 0 and we get the following system of linear equations.

$$
\begin{aligned}
0 \;=\; & -P_{a,b}\left(\frac{b}{T_h} + ab\nu_h + a\nu_f f + \frac{n-(a+b)}{2T_c}\right) \\
& + P_{a+1,b-1}(a+1)\nu_f f + P_{a-1,b-1}\frac{n+2-(a+b)}{2T_c} \\
& + P_{a-1,b+1}\frac{b+1}{T_h} + P_{a+1,b+1}(a+1)(b+1)\nu_h \qquad (4)
\end{aligned}
$$

with the boundary conditions (3). The system (4) is too large to deal with explicitly. Indeed, it has of the order of $n^2/4$ equations since there is one equation for every state of the dynamics; and the states are lattice points filling a triangular shape that is exactly one half of a square with sides $n\sqrt{2}$. However, the system (4) can be solved numerically using computer software packages like MAPLE. The system can be also solved analytically for some special cases.

5. The uptake rate

The proportion of handlers in the population is given by

$$
f(n) = \frac{1}{n}\sum_{b=0}^{n} b \cdot \sum_{a} P_{a,b}\,. \qquad (5)
$$

The function $f(n)$ is a measure of the uptake rate in the population of n individuals, [9]. After conducting the numerical experiments, we conclude that the function depends on the following three factors only

- the size of the population, n ,
- the product $(\nu_f f Th)$,
- the product $(\nu_h Tc)$.

The second factor corresponds to up-down movement in the diagram (searching food and eating), the third factor corresponds to left right movement on the diagram (looking for a handler and the fighting). Consequently, we may restrict ourselves to fixing $Th = 1$ and $Tc = 1$ and changing $\nu_f f$ and ν_h only.

6. Dependence of the uptake rate on ν_h

Notice that with the increasing ν_h , the uptake rate becomes sensitive to the population size being odd or even. When ν_h is relatively small, then $f(n)$ is a decreasing function of population size. As ν_h becomes a bit larger, yet not too large, f has a local maximum at $n = 3$ and is decreasing for $n \geq 3$. As ν_h gets even larger, f starts to have local maxima at $n = 3, 5, \ldots$, and eventually becomes a monotone function. When ν_h gets very large, there is a significant dependence of the uptake rate on the parity of the population size. Figure 4 shows the behavior of $f(n)$ for a range of values of ν_h .

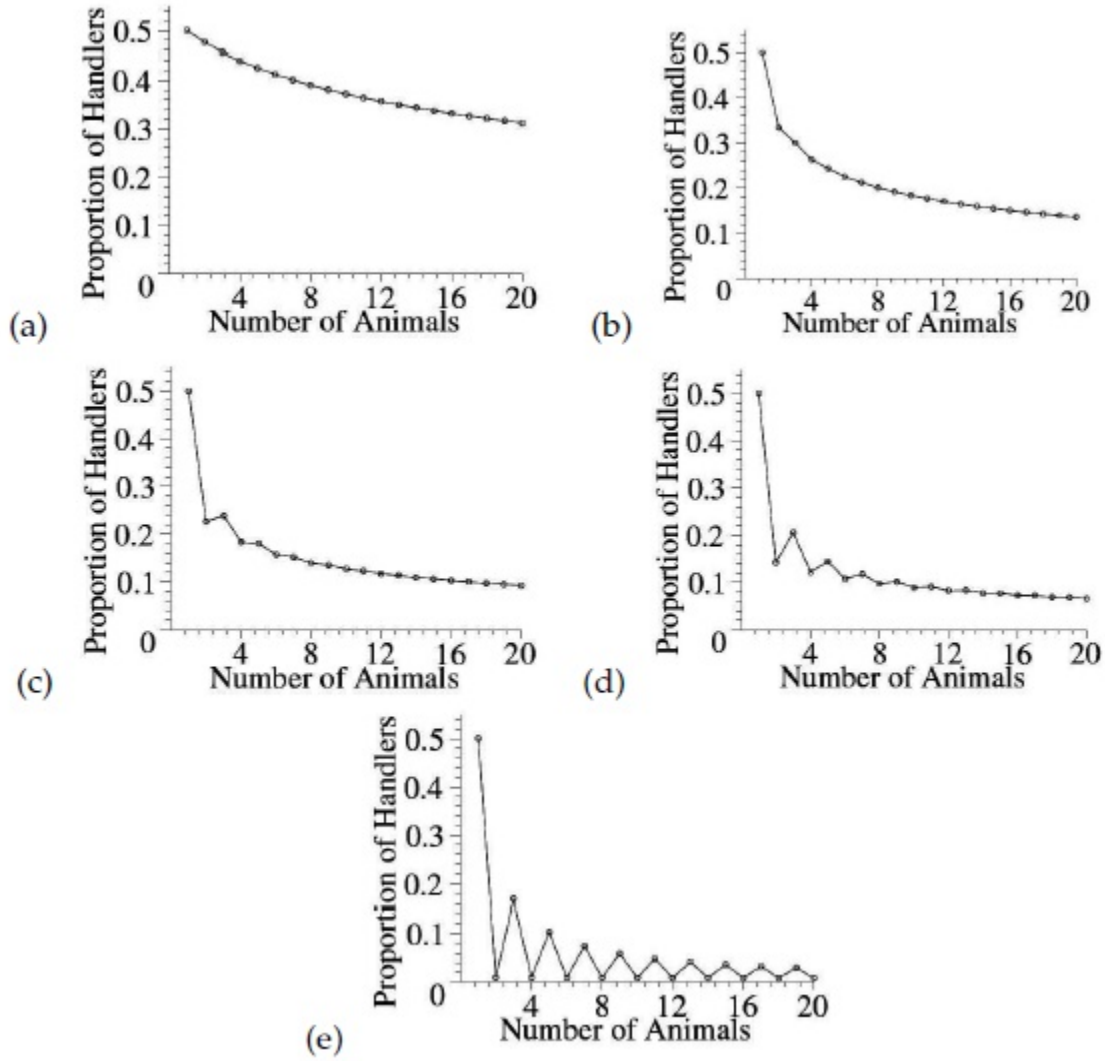

Figure 4. Uptake rates for kleptoparasitic populations depends on vh. (a) vh = 0.1 , (b) vh = 1 , (c) vh = 2.4 , (d) vh = 5 , (e) vh = 100. Other parameter values are vf f = 1 , Th = 1 , Tc = 1

6.1 *The situation for large* v*h*

When v*h* is large, then the dynamics is pushed towards the right hand side of the diagram on Figure 2. The exact shape of the right hand side depends on the parity of the population size and it is given in the Figure 5.

When *n* is even and v*h* is large, the population is almost always in the state (0, 0) , i.e., all individuals fighting. This means that the uptake rate is approximately 0 .

When *n* is odd and v*h* large, the population is either in (1, 0) or in (0, 1) , i.e., *n* - 1 individuals are engaged in fights and the remaining one is either searching or handling. This yields the following system of linear

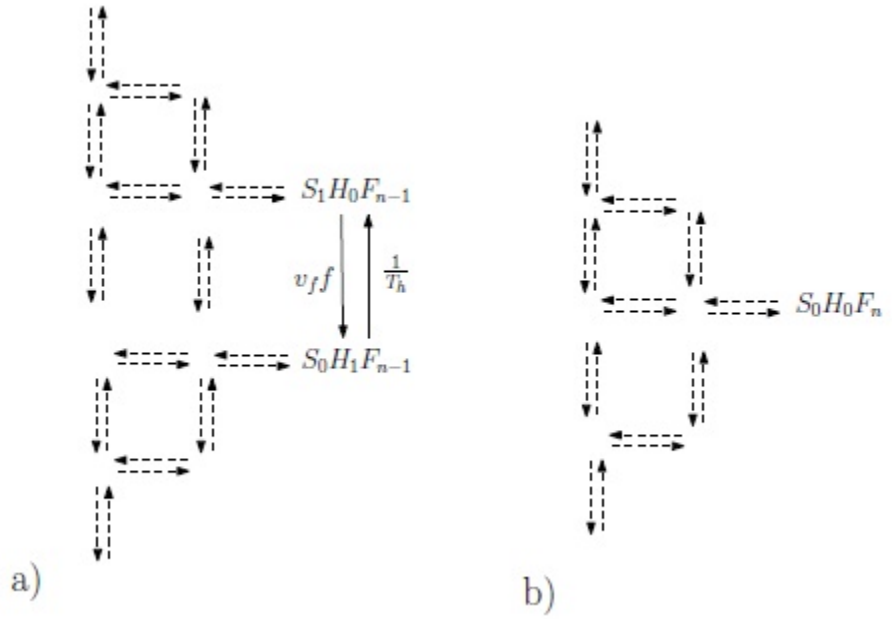

Figure 5. Right end of the scheme of the dynamics, (a) for odd *n* ; (b) for even *n*

Equations

$$P_{0,1} + P_{1,0} = 1, \tag{6}$$

$$-P_{1,0}\nu_f f + \frac{1}{T_h} \cdot P_{0,1} = 0 \tag{7}$$

and we also have

$$f(n) = \frac{1}{n} P_{0,1} .$$

The equation (7) gives

$P0,1 = \nu f f \cdot Th \cdot P\nu,1$

and, by (6), we get

$$f(n) = \begin{cases} \frac{\nu_f f T_h}{n(1+\nu_f f T_h)}, & n \text{ is odd,} \\ 0, & \text{otherwise.} \end{cases}$$

6.2 *The situation for small* ^{o}h

When v*h* ≈ 0 , then the individuals stay only in the left part of the diagram on Figure 2 since there are no fights. Hence, *Pa,b* 6≠ 0 only if 0 ≤ *a* = *n* - *b* ≤ *n* . Consequently, we have to solve the system

$$0 = -(n-b)\nu_f f P_{n-b,b} + \frac{b+1}{T_h} P_{n-b-1,b+1}, \quad b = 0, \ldots, n, \qquad (8)$$

$$1 = \sum_{b=0}^{n} P_{n-b,b}. \qquad (9)$$

Iteratively applying (8) yields

$$P_{n-b,b} = \frac{n!}{(n-b)!b!}(\nu_f f T_h)^b P_{n,0} \qquad (10)$$

and, by (9) we get

$$\begin{aligned} f(n) &= \frac{1}{n}\sum_{b=0}^{n} b \cdot P_{n-b,b} \\ &= \frac{1}{n(1+\nu_f f T_h)^n}\sum_{b=0}^{n} b\frac{n!}{(n-b)!b!}(\nu_f f T_h)^b \\ &= \frac{\nu_f f T_h}{(1+\nu_f f T_h)}. \end{aligned}$$

The above is actually an expression for the population with no fights as derived in [15]. Notice that when there are no fights, the proportion of handlers does not depend on the population size *n*.

6.3 *Population of n* = 2 *versus n* = 3

When *n* = 1, 2, 3 we can solve the dynamics (4) by hand to get

$$\begin{aligned} f(1) &= \frac{\nu_f f T_h}{\nu_f f T_h + 1}, \\ f(2) &= \frac{\nu_f f T_h \cdot (1+\nu_f f T_h)}{2\nu_f f T_h \cdot \nu_h T_c + (1+\nu_f f T_h)^2}, \\ f(3) &= \frac{\nu_f f T_h \cdot (2\nu_f f T_h \cdot \nu_h T_c + (1+\nu_f f T_h)^2)}{(1+\nu_f f T_h)(6\nu_f f T_h \cdot \nu_h T_c + (1+\nu_f f T_h)^2)}. \end{aligned}$$

Clearly,

f (1) > max*f f* (2), *f* (3)*g*

for any parameter values (there is an equality if v*h* = 0 , i.e., no fights).

The inequality can be seen heuristically from the fact that once there are at least 2 individuals, there is a nonzero chance they will engage in a fight and thus it will lower the uptake rate. After some algebraic manipulation, we get that $f(2) > f(3)$ whenever

$$\nu_h T_c < \frac{(1+\nu_f f T_h)^2}{2\nu_f f T_h}. \qquad (11)$$

The numerical experiments moreover show that if (11) holds, then the uptake rate is monotonically decreasing.

7. Dependence of the uptake rate on z*f f*

As can be seen already from (11), the behavior of the uptake rate depends on both v*hTc* and v *f f Th* . The dependence is unfortunately highly nonlinear. Nevertheless, assuming, without loss of generality, $Tc = Th = 1$, we can derive from (11) the following qualitative behavior. If v$ff \approx 0$, then (11) holds for most of the values of v*h* and hence $f(n)$ is a decreasing function of the population size. The same is true if v$ff \approx \infty$. For a fixed v*h* , as v*f f* increases from 0 to a threshold value V , the behavior of $f(n)$ changes from decreasing to slightly zigzag (with local maxima at $n = 3$, then at $n = 3$ and $n = 5$, etc.) to a significantly zigzag functions with local minima at even n and local maxima at odd n . As v*f f* gets above the threshold V , then f starts to flatten out fromvery zigzag to monotonically decreasing and eventually becomes almost constant 1 (for very large v*f f*).

The behavior is demonstrated at the Figure 6.

The threshold value V depends on the value of v*h* . However, we did not find an explicit formula for this dependence, partially for we did not quantify the zigzag behavior (for example by measuring the oscillation of f) explicitly.

8. Conclusions

We have seen that there is a vast literature on mathematical modeling of kleptoparasitism. We have reviewed significant papers on deterministic models and have seen that, starting from the paper [9], the model assumptions have become progressively closer to biological reality by allowing the individuals to exhibit a wider range of behavior, by varying the food types, and by allowing group fights over the same food item. Nevertheless, there was one key assumption — infinite population size — that remained untouched until very recently. Currently, there is only one published paper, [29], and one preprint, [22], that deal with kleptoparasitism in finite populations.

Since actual populations of kleptoparasitic organisms are likely to follow the dynamics of finite rather than infinite populations, modeling kleptoparasitism in finite populations is an important problem to be addressed and solved theoretically. In this paper, we have studied the model introduced in [29]. We provided the analytical solutions for sizes $n = 1, 2, 3$ and wrote a system of linear equations that can be solved numerically for any population size.

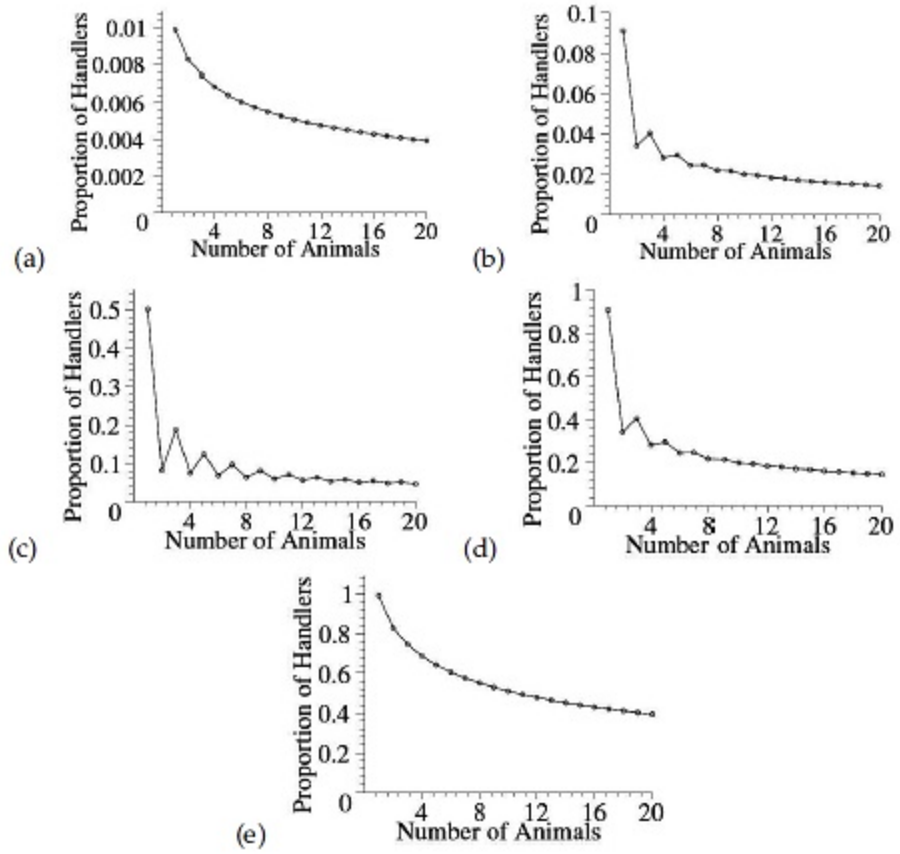

Figure 6. Uptake rates for kleptoparasitic populations depends on vf . (a) vf = 0.01 , (b) vf = 0.1 , (c) vf = 1 , (d) vf = 10 ,(e) vf = 100 . Other parameter values are vh = 10 , Th = 1 ,Tc = 1

Currently, with Dr. M. Broom (University of Sussex, UK), we are working on formalizing the methods (detailed balance conditions for Markov chains) introduced informally in [22] and we hope that this will yield an analytical solution and further insight in the dynamics.

From the numerical experiments, we could see that the qualitative behavior of the uptake rate function depends mostly on the situation in populations of 2 and 3 individuals. If the individuals do better in the population of 3 than in 2 , it means that the parameters are set for an old saying: “If two dogs fight for a bone, the third one runs away with it”, [22]; in which case an uptake rate function has a zigzag behavior with lows for even population sizes and ups for odd population sizes. It should be noted, however, that, for any parameter values, the uptake rate function eventually become a monotonically decreasing function when n is large enough.

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